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ARTICLE

Morphological variation of the leaves of *Aechmea distichantha* Lem. plants from contrasting habitats of a Chaco forest: a trade-off between leaf area and mechanical support

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ABSTRACT: (Morphological variation of the leaves of *Aechmea distichantha* Lem. plants from contrasting habitats of a Chaco forest: a trade-off between leaf area and mechanical support). Several authors have reported phenotypic plasticity for bromeliad plants growing in contrasting habitats. Morphological and physiological differences of leaves seem to be an adaptation to water and light use, but there is also a compromise between carbon gain and the costs of sustaining static and dynamic loads. We hypothesized that plastic responses to habitat at the leaf level represent a trade-off between the photosynthetic area for capturing light and mechanical support. In this study, we measured morphological and architectural variables of central and basal leaves of *Aechmea distichantha* plants from the understory and forest edge, as well as anatomical variables of plants from each habitat. Understory plants had longer leaves, larger blade areas and greater length/width ratios than forest-edge plants. Blades of understory plants were less erect, less succulent, had thicker fiber tissue surrounding the vascular bundles and a higher curvature index than blades of forest-edge plants. Thus, understory plants increased their flexural stiffness by modifying their tissue structure as well as the shape of their leaves. On the other hand, blades of forest-edge plants had higher stomatal density and higher trichome density on their adaxial sides than understory plants. These patterns could be adaptations for higher gas exchange and to reduce vulnerability to photoinhibition in sun plants when compared to shade plants. Finally, most of the morphological and architectural variables were significantly different between positions. These results support our view that there is a trade-off at the leaf level between photosynthetic leaf area (for light capture and water use) and mechanical support.

Key words: biomechanics, bromeliads, leaf anatomy, leaf morphology, phenotypic plasticity.

RESUMO: (Variações morfológicas de folhas de plantas de *Aechmea distichantha* Lem. de habitats contrastantes de uma floresta do Chaco: uma compensação entre área foliar e suporte mecânico). Diferenças morfológicas e fisiológicas em nível foliar parecem ser uma adaptação ao uso da água e luz, mas também existe uma compensação entre o ganho de carbono e os custos de sustentar cargas estáticas e dinâmicas. Nossa hipótese é que as respostas plásticas ao habitat no nível foliar representam uma compensação entre a área fotossintética para a captação de luz e apoio mecânico. Neste estudo, medimos variáveis morfológicas e arquitetônicas nas folhas centrais e basais de plantas de *Aechmea distichantha*, de sub-bosque e das bordas da floresta, assim como as variáveis anatômicas de plantas de cada habitat. Lâminas foliares de plantas do sub-bosque foram menos eretas, menos suculentas, com contendo fibras de pearedes espessadas em torno dos feixes vasculares e índice de curvatura maior do que as plantas das bordas da floresta. Assim, plantas de sub-bosque aumentaram sua rigidez à flexão, modificando sua estrutura de tecidos, bem como a forma de suas folhas. Por outro lado, as lâminas foliares de plantas de borda da floresta apresentaram maior densidade estomática e maior densidade de tricomas em sua face adaxial do que as plantas de sub-bosque. Esses padrões podem ser adaptações para um intercâmbio maior de gás e redução da vulnerabilidade a fotoinibição no sol do que em plantas de sombra. Finalmente, a maior parte das variáveis morfológicas e arquitetônicas foram significativamente diferentes entre as posições. Estes resultados suportam nossa opinião de que há uma compensação, no nível da folha, entre a área foliar fotossintética (para a captação de luz e uso da água) e suporte mecânico.

Palavras-chave: anatomia foliar, biomecânica, bromélias, morfologia foliar, plasticidade fenotípica.

INTRODUCTION

A large variety of organisms express phenotypic plasticity in response to different environments (Miner *et al.* 2005 and references therein). Phenotypic plasticity is the ability of an organism to produce different phenotypes in response to environmental changes (Evans 1972, DeWitt *et al.* 1998, Miner *et al.* 2005, Valladares *et al.* 2007, Auld *et al.* 2010). According to the Optimal Partitioning Theory, plants respond to these environmental variations by allocating biomass among several plant organs to optimize the capture of light, water, nutrients, and carbon dioxide in order to maximize their growth rate (Bloom *et al.* 1985). These plastic responses are expressed at different levels ranging from variations in plant morphology, anatomy, or physiology to alterations in growth, behavioral repertoires, and even life history and demography (Schlichting & Pigliucci 1998, Chambel *et al.* 2005, Miner *et al.* 2005, Valladares *et al.* 2006, 2007).

Phenotypic plasticity for plants growing in contrast-

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ing habitats (i.e., sun vs. shade) has long been studied for plants in general (Hutchings & de Kroon 1994, Rozendaal *et al*. 2006) and for bromeliads in particular (Lee *et al.* 1989, Cogliatti-Carvalho *et al*. 1998, Scarano *et al*. 2002, Freitas *et al*. 2003, Skillman *et al*. 2005, Lenzi *et al*. 2006, Mantuano & Martinelli 2007, Cavallero *et al*. 2009). Bromeliad plants growing in the understory allocate a larger amount of resources to develop a larger photosynthethic area and thus may capture the low photon density found in the understory (Lee *et al*. 1989, Skillman *et al*. 2005, Mantuano & Martinelli 2007, Cavallero *et al*. 2009). The loose array of their leaves allows them to maximize the reduction of overlapping leaves and self-shading (Scarano *et al*. 2002), and thus maximizes the photosynthetically active area. In contrast, the morphology of plants growing in open areas reduces exposure to light. The higher number of leaves would produce a larger amount of leaf overlapping, thus creating a structure that avoids high light stress by reducing the light intensity that could affect chlorophyll (Freitas *et al*. 2003, Cavallero *et al*. 2009). Sun plants probably experience higher evaporative rates because they are exposed to significantly higher irradiance, temperature and wind speeds (Cavallero *et al.* 2009).

Phenotypic plasticity studies at the plant level do not take into account the differences between individual leaves (Krauss 1948-1949, Valladares & Pugnaire 1999, Benzing 2000, Zotz *et al*. 2002). Morphological and physiological differences at the leaf level seem to be an adaptation to water and light use (Benzing 2000). However, leaf design also implies a compromise between carbon gain and the costs of sustaining static and dynamic loads (Niklas 1997, Read & Stokes 2006). Understory plants may reduce bending loads by increasing their flexural stiffness (King *et al*. 1996, Niklas 1997, Huber *et al*. 2008), which could be achieved either by increasing the Young's moduli (i.e., a measurement of the rigidity of a material), the second moment of area (i.e., a measurement of the degree to which the cross-sectional area of a support contributes to mechanical stability), or both (King *et al*. 1996, Niklas 1997, Huber *et al*. 2008). For bromeliads, in particular, understory plants may increase the structural stiffness of their leaves by producing a higher proportion of fibers at the expense of parenchyma (de Oliveira *et al*. 2008), by corrugation of their leaves (Krauss 1948-1949) or by having channeled blades instead of flat blades (Benzing 2000).

There may also be differences between leaves located at different positions within a plant (Krauss 1948-1949, Valladares & Pugnaire 1999, Benzing 2000, Zotz *et al*. 2002). For bromeliads, it is known that central leaves are longer and more erect than basal leaves (Benzing 2000, Zotz *et al*. 2002). The former also have higher photosynthetic values because they are younger and are frequently exposed to higher light conditions than basal leaves (Zotz *et al*. 2002). It is likely that central leaves have higher mechanical support than basal leaves, but to our knowledge this has not been reported for bromeliads.

In a recent study of *Aechmea distichantha* Lem. (Bromeliaceae), we recorded phenotypic plasticity at the plant level for individuals growing in an open xerophytic Chaco forest (Cavallero *et al*. 2009). Previously, Smith & Downs (1974) reported that this species grows leaves that are 4-5 times longer in shade than in sun, but no data were available to indicate the anatomical differences between the sun and shade leaves. Thus, in the present study, we used plants of this species growing along forest edges and in the understory of a xerophytic Chaco forest to further explore phenotypic plasticity at the leaf level. We evaluated morphological, architectural and anatomical plastic responses of individual leaves from two contrasting positions (i.e., central and basal leaves). We hypothesized that these plastic responses to habitat at the leaf level represent a compromise between photosynthetic area (i.e., for light capture) and mechanical support.

MATERIALS AND METHODS

Study area and analyzed species

The study was carried out in a 400-ha stand of the *Schinopsis balansae* Engl. forest type (*quebrachal*, Lewis 1991, Lewis *et al.* 1997) located at Las Gamas, in Santa Fe, Argentina (Estación Experimental Tito Livio Coppa, 29°28'S, 60°28'W, 58 m a.s.l.). The climate is humid, with a mean annual temperature of about 20 °C, and mean annual precipitation of about 1000 mm. Rainfall is concentrated in the summer (December – March) and a dry season of variable length occurs in the winter. The forest is located on a mosaic of soils with low hydraulic conductivity and high sodium content (Espino *et al*. 1983), and the soil surface has a noticeable microrelief (Barberis *et al.* 1998). In these forests, most woody species are deciduous, with small leaves, and frequently have spiny structures (Lewis *et al*. 1997). The structure and floristic composition change markedly in tens of meters in relation to differences in microtopography and soil moisture. Areas with convex topography have higher tree and shrub densities than plain areas (Barberis *et al*. 2002). Within convex areas of the *quebrachal*, the vegetation heterogeneity is related to the presence of populations of two prickly bromeliads: *Bromelia serra* Griseb. and *Aechmea distichantha* (Barberis & Lewis 2005). Both species inhabit the forest understory, but they are frequently found along the forest edges and in open areas.

Aechmea distichantha occurs as a terrestrial or epiphytic plant in deciduous, semideciduous and evergreen forests from sea level to 2400 m elevation in southern Brazil, Bolivia, Paraguay, Uruguay, and northern Argentina (Smith & Downs 1979). It is a tank-forming bromeliad (Ecophysiological Type III *sensu* Benzing

2000) with channeled leaves that are usually 30-100 cm long and arranged in a very dense rossette. The sheaths are elliptic or oblong, and have entire borders, while the blades are narrowly triangular, pungent, with borders armed with stout dark spines, which are 4 mm long (Smith & Downs 1979). The leaves are hypostomatic and present sinuous epidermal cell walls with silica bodies (Derwidueé & González 2010). There are trichomes on both adaxial and abaxial surfaces (Proença & Sajo 2004). The chlorenchyma has air channels filled with irregular star-shaped cells. The water parenchyma is well developed, formed by 2-4 layers of cells that represent 25-40% of the mesophyll in the apical region, up to 50% of the mesophyll in the middle region and even 60-70% in the basal region of a blade. In contrast, the mesophyll represents only 20-40% of the sheath (Proença & Sajo 2004). Plants reproduce both sexually and asexually (Smith & Downs 1979), but the latter is predominant in the forest were the plants were studied. Ramets from one genet exposed to different environmental conditions may show different phenotypes (i.e., modular plasticity *sensu* de Kroon *et al*. 2005). In the *quebrachal*, like in other ecosystems (Cogliatti-Carvalho *et al*. 1998), there is a morphological gradient of this species between modules completely exposed to sun or shade conditions with a full set of intermediate phenotypes along this light gradient (IM Barberis, pers. observ.).

Sampling procedure

In November 2004, we extracted 7 plants in vegetative phenological state from the understory and 8 plants

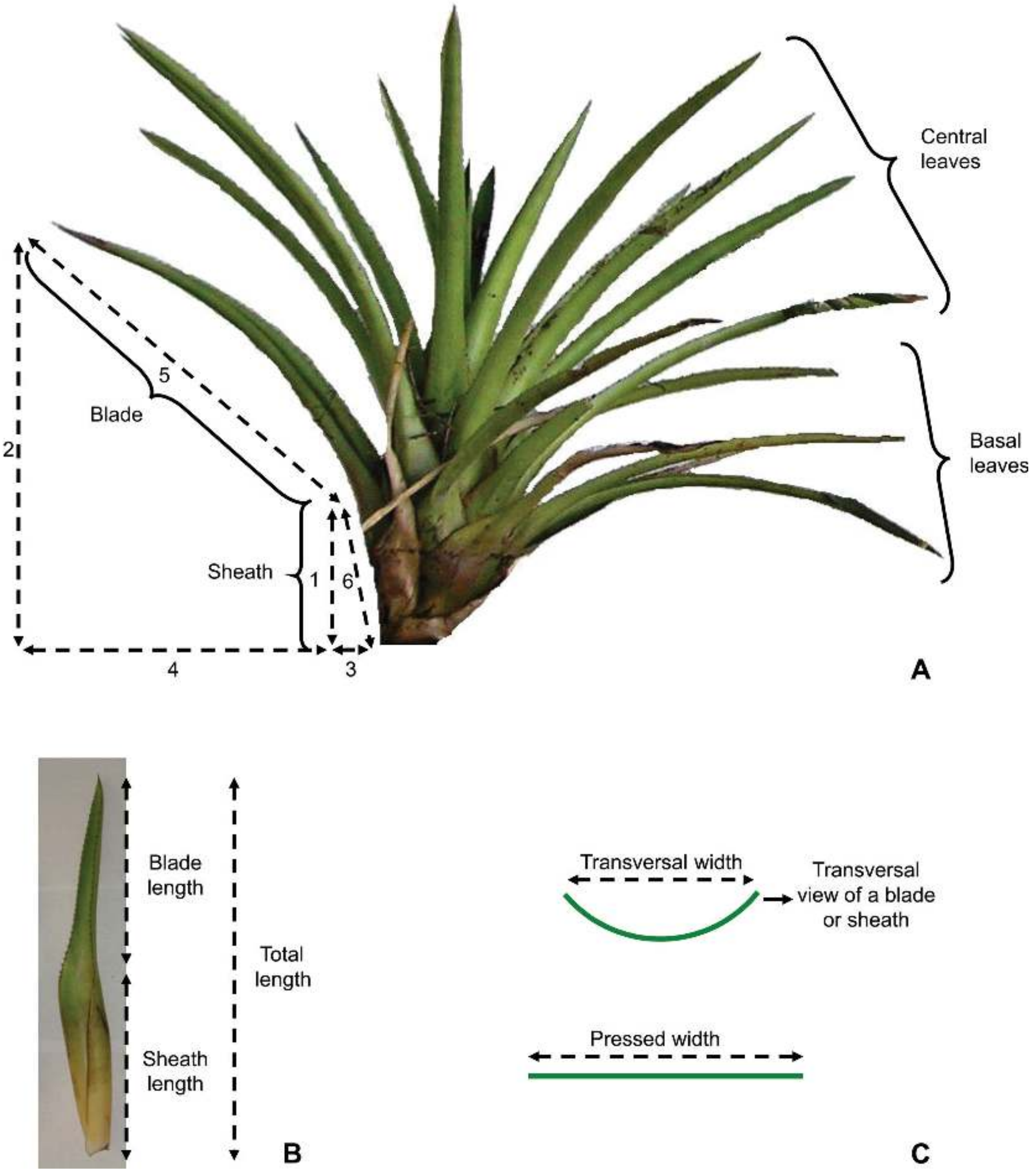

Figure 1. Measurements of *Aechmea distichantha*. **A.** Plant showing basal and central leaves and the six distances measured (dashed lines); **B.** Leaf showing total length and blade and sheath lengths; **C.** Transversal scheme of a leaf showing its transversal and pressed width.

from the forest edge. The selected ramets were at least 5 m from each other to assure genet independence. Plants were carefully removed and taken to the lab. Plants from both habitats were approximately the same size (Sun plants: median = 140.3 g dry biomass, range = 24.8-179.0 g; Understory plants: median = 124.8 g dry biomass, range = 92.0-244.1 g; Mann Whitney test: W = 60.0, $P = 0.685$) to control for apparent phenotypic plasticity (Cavallero *et al*. 2009).

From each plant we selected the two longest leaves (hereafter called central leaves) and two leaves from the lowest part of the plant, which were not rotten or senescing (hereafter called basal leaves). For each selected leaf, we measured six distances using a vertical level and a measuring tape in order to determine the angle of its sheath and blade (Fig. 1A). The blade and sheath angles were calculated as the average of the results from three trigonometric functions: arcsin, tangent and cosine.

For each selected leaf, we measured its total length (cm), as well as the length of its blade and sheath (cm) (Fig. 1B). For each blade and sheath, we measured the transversal width (i.e., width on the adaxial side from one margin to the other without pressing it; cm), and the pressed width (i.e., width of the pressed blade or sheath; cm) (Fig. 1C). Then, we estimated a curvature index as CI = (pressed width – transversal width)/pressed width.

In order to calculate the Succulence index (SI = (Saturated biomass – Dry biomass)/Area), we removed a 1 cm long cross section (i.e., from one margin to the other) at the halfway point of the length of each blade and sheath (Schmidt & Zotz 2001). Each blade or sheath cross section was kept in a zipped plastic bag within a water saturated atmosphere for twelve hours and then weighed (SCALTEC SBA 52, d = 0.01 g, Germany) to obtain the saturated biomass. We outlined the cross sections on paper, and then we cut and weighed the paper outlines (SCALTEC SBA 32, d = 0.0001 g, Germany) to estimate their areas using the gravimetric method (Freitas *et al*. 2003). Then, the cross sections were oven dried at 70 ºC to a constant weight to obtain their dry biomass.

Finally, each blade and sheath was pressed and outlined on paper, and their areas were estimated using the gravimetric method (Freitas *et al*. 2003). Then, the blades and sheaths were oven-dried at 70 ºC to constant weight (SCALTEC SBA 52, d = 0.01 g, Germany). The values of the removed cross sections were added to complete the blade and sheath area and biomass. We also derived the following variables: Length/width ratio of blades and sheaths (cm/cm) and Sheath proportion as (sheath length × 100)/total leaf length (%).

In November 2005, we selected five pre-adult plants (i.e., plants which had not flowered yet) from the understory and six plants of similar size from the forest edge in the same study area. For each individual, we harvested the longest leaf, removed a cross section from the middle third of its blade, and fixed the material in FAA (i.e., formalin, alcohol, acetic- acid). Handmade cross sections were diaphanized according to Strittmatter (1973) and stained with safranine/fast-green (D'Ambrogio de Argüeso 1986). Width and number of layers of chlorophyll parenchyma and water parenchyma of the middle third of the blade were measured for 79 replicates from six forest-edge plants, and 42 replicates from four understory plants. Tissue thickness was determined under a light microscope. Thickness of the fiber tissue surrounding the vascular bundles was measured for 20 replicates from four forest-edge plants and from four understory plants. Trichome and stomatal densities were determined near the middle of the blade for ten replicates from six individuals of the forest edge and five individuals from the understory.

Data analyses

Differences in leaf morphology and architecture between habitats and position of leaves within the plant were analyzed with a partly nested design with habitat (i.e., understory vs. forest edges), as principal effects, and leaf position (i.e., basal vs. central) nested within the plant effect, as a secondary effect. The habitat and position effects were analyzed with General Linear Mixed Models (PROC MIXED, SAS Version 8.0, Littell *et al*. 1996). Treatment effects (i.e., habitat and position) were considered as fixed, while plant effect (nested within habitat) was considered random. F tests were carried out considering Type III Sum of Squares (Littell *et al*. 1996). Data were analyzed for residual normality (Anderson-Darling) and homoscedasticity (Levene) (Quinn & Keough 2002). For each plant we averaged the values of leaves within each position. Leaf length, blade and sheath lengths, blade and sheath widths and blade and sheath areas were $\log_{10}$-transformed to improve normality and homoscedasticity. The remaining variables were not transformed.

Differences in leaf thickness (chlorophyll and water parenchyma), and in thickness of fiber tissue surrounding the vascular bundles between forest-edge and understory plants were analyzed with the Welch two sample *t*-test, whereas differences in stomatal and trichome densities between habitats were analyzed with the U Mann-Whitney test (Quinn & Keough 2002). For all these analyses, replicates within each individual were averaged.

RESULTS

Leaf morphology, architecture and anatomy of individuals grown in understory vs. forest edges

Plants grown in the understory had longer leaves due to longer blades and sheaths than those from plants grown in forest edges (Fig. 2 and 3; Tab. 1). However, understory plants had lower sheath proportion than forest-edge plants (Fig. 2; Tab. 1). There were no differences in blade or sheath widths between habitats, thus understory plants had greater blade and sheath length/

Table 1. Results of linear mixed models for leaf, blade, and sheath variables with treatments (i.e., habitat and position) as fixed effects and plants as a random effect for basal and central leaves of *Aechmea distichantha* plants from the understory and forest edge. For each variable, units and transformation used are shown. Numerator and denominator degrees of freedom, F-values and significance are shown. Bold values denote significant differences.

Sampling unit	Variable	Unit	Transformation	Habitat		Position		Habitat x Position	
				$F_{1,13}$	P	$F_{1,13}$	P	$F_{1,13}$	P
Leaf	Total length	cm	$\log_{10}$	62.05	<**0.0001**	46.67	**<0.0001**	1.43	0.2536
	Sheath proportion	cm/cm		33.82	<**0.0001**	5.08	**0.0422**	0.06	0.8153
Blade	Length	cm	$\log_{10}$	61.19	<**0.0001**	22.42	**0.0004**	0.60	0.4527
	Width	cm	$\log_{10}$	0.04	0.8419	39.61	**<0.0001**	16.13	**0.0015**
	Length/width ratio	cm/cm		174.85	<**0.0001**	32.18	**<0.0001**	14.48	**0.0022**
	Area	cm^2	$\log_{10}$	7.74	**0.0155**	17.86	**0.0010**	0.15	0.7075
	Curvature index	cm/ cm		10.60	**0.0063**	0.09	0.8701	2.44	0.1423
	Angle			6.41	**0.0250**	19.55	**0.0007**	0.61	0.4494
	Succulence index	g/cm2		15.13	**0.0037**	0.07	0.7962	0.31	0.5940
Sheath	Length	cm	$\log_{10}$	14.96	**0.0019**	49.38	**<0.0001**	10.88	**0.0058**
	Width	cm	$\log_{10}$	0.09	0.7630	69.80	**<0.0001**	9.03	**0.0101**
	Length/width ratio	cm/cm		46.06	<**0.0001**	0.56	0.4662	2.45	0.1416
	Area	cm^2	$\log_{10}$	10.91	**0.0057**	0.16	0.6982	7.59	**0.0164**
	Curvature index	cm/ cm		15.57	**0.0017**	48.63	**<0.0001**	1.08	0.3172
	Angle	°		0.00	0.9611	7.57	**0.0165**	0.34	0.5681
	Succulence index	g/cm^2		2.66	0.1270	9.98	**0.0075**	1.56	0.2331

width ratios and also greater blade and sheath areas than forest-edge plants (Fig. 3; Tab. 1).

Forest-edge plants had greater blade angles (i.e. more erect blades), but similar sheath angles than understory plants (Fig. 4; Tab. 1). Blades of forest-edge plants were more succulent and had a lower curvature index than blades of understory plants (Fig. 4). Similarly, sheaths of forest-edge plants had a lower curvature index than sheaths from understory plants. However, there were no differences in the sheath succulence index between habitats (Fig. 4; Tab. 1).

There were significant differences in mesophyll thickness between habitats (forest edges = 1487 ± 52 µm / understory = 1078 ± 19 µm; *t* value = 7.41, P = 0.0002) due to significant differences in chlorophyll parenchyma thickness (forest edges = 840.7 ± 24 µm / understory = 635.0 ± 29 µm; *t* value = 5.43, P = 0.002), but not in the water parenchyma thickness (forest edges = 646.7 ± 66 µm / understory = 519.2 ± 24 µm; *t* value = 1.81, P = 0.120) (Fig. 5A, 5B). The chlorophyll parenchyma of forest-edge plants had larger cells than the one from understory plants (forest edges = 44.4 ± 2.06 µm / understory = 34.9 ± 2.25 µm; *t* value = 3.12, P = 0.011) (Fig. 5A, 5B). Blades of forest-edge plants had thinner fiber tissue surrounding the vascular bundles than those blades of understory plants (forest edges = 21.8 ± 3.2 µm / understory = 38.8 ± 1.9 µm; *t* value = -4.58, P = 0.006) (Fig. 5C, 5D).

Blades of forest-edge plants had higher stomatal density than those from understory plants (median: 19 stomata/mm^2 vs. 15 stomata/10 mm^2, respectively; W = 40.0, P < 0.01, N = 5 for each habitat). Similarly, blades of forest-edge plants had higher trichome density on their adaxial side (median: 8 trichomes/mm^2 vs. 6 trichomes/mm^2; W = 40, P < 0.01, N = 5 for each habitat), but lower trichome density on their abaxial side (median: 9 trichomes/mm^2 vs. 13 trichomes/mm^2; W = 15, P < 0.01, N = 5 for each habitat) than those from understory leaves.

Morphology of leaves from different positions within a plant

In both habitats, central leaves were longer, but had a lower sheath proportion than basal leaves (Fig. 2; Tab. 1). Blades from central leaves were longer, wider, had

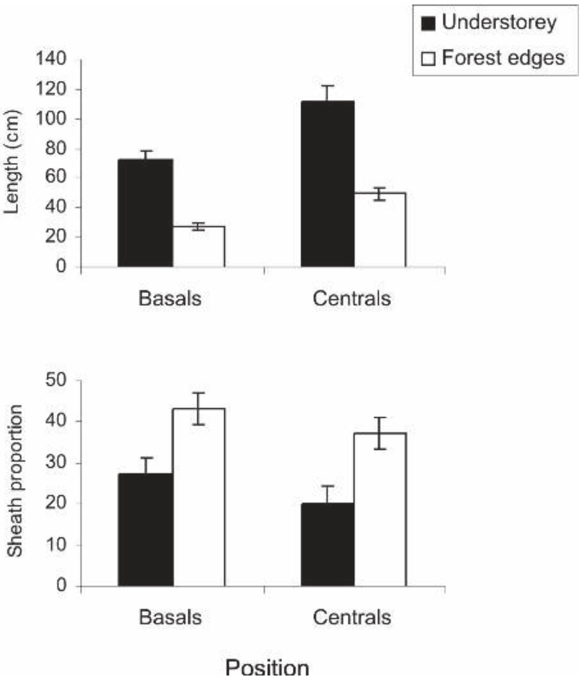

Figure 2. Length and sheath proportion (mean ± s.e.m.) of basal and central leaves of *Aechmea distichantha* plants from the understory and forest edge.

higher length/width ratio and area than those from basal leaves (Fig. 3; Tab. 1). Sheaths from central leaves were longer and wider than sheaths from basal leaves, but there were no differences in sheath length/width ratio or area between leaf positions (Fig. 3; Tab. 1).

Blades and sheaths from central leaves were more erect than those from basal leaves (Fig. 4; Tab. 1). There were no differences in blade succulence or curvature index between leaves from different positions (Fig. 4; Tab. 1). In contrast, sheaths from central leaves were more succulent and had a higher curvature index than those from basal leaves (Fig. 4; Tab. 1).

DISCUSSION

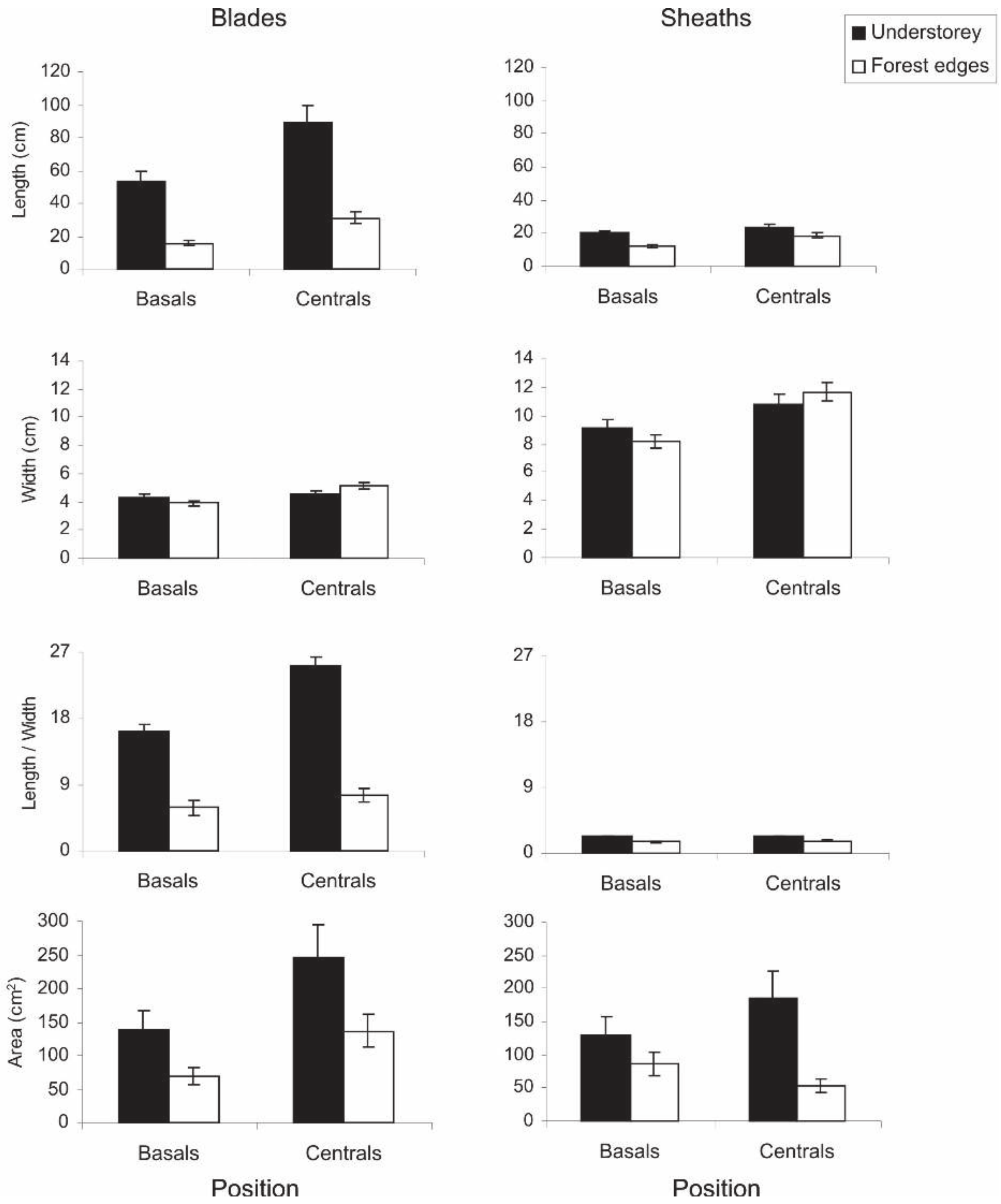

Figure 3. Length, width, length/width and area (mean ± s.e.m.) of blades and sheaths from basal and central leaves of *Aechmea distichantha* plants from the understory and forest edge.

Leaf morphology, architecture and anatomy of individuals grown in understory vs. forest edges

In the understory, *A. distichantha* plants had significantly longer leaves, blades and sheaths than individuals along the forest edge. Furthermore, understory leaves had a greater length/width ratio, which is directly related to the greater blade and sheath area. Similar results were recorded for leaves of other bromeliad species with populations growing in contrasting habitats (Benzing 2000, Lenzi *et al*. 2006). The increase of the photosynthetic active area at the leaf level is a typical response to light (Evans 1972), which increases the ability of the leaf to capture the scarce photons in shady environments (Benzing 2000, Scarano *et al*. 2002).

Some results of this study at the leaf level agree with results of our previous study at the plant level (Cavallero *et al*. 2009). For instance, longer leaves in the understory led to taller plants with larger diameters (Cavallero *et al*. 2009). However, in our previous study there were no significant differences at the individual level in total blade area or total blade biomass between understory and forest-edge plants, despite understory plants having a greater projected leaf area (Cavallero *et al*. 2009). It is likely that these discrepancies could be related to a higher leaf angle in forest-edge plants (i.e., more erect leaves; as recorded in this study and suggested by Lee *et al*. 1989 and Scarano *et al*. 2002) and/or to a higher number of leaves in forest-edge plants (Cavallero *et al*. 2009).

Forest-edge plants had significantly more erect blades (i.e., greater angles with respect to the ground) than understory plants. This leaf display allows for the reduction of excessive radiation (Benzing 2000) and thus decreases the risk of overheating and photo-oxidative destruction of the photosynthetic apparatus (Val-

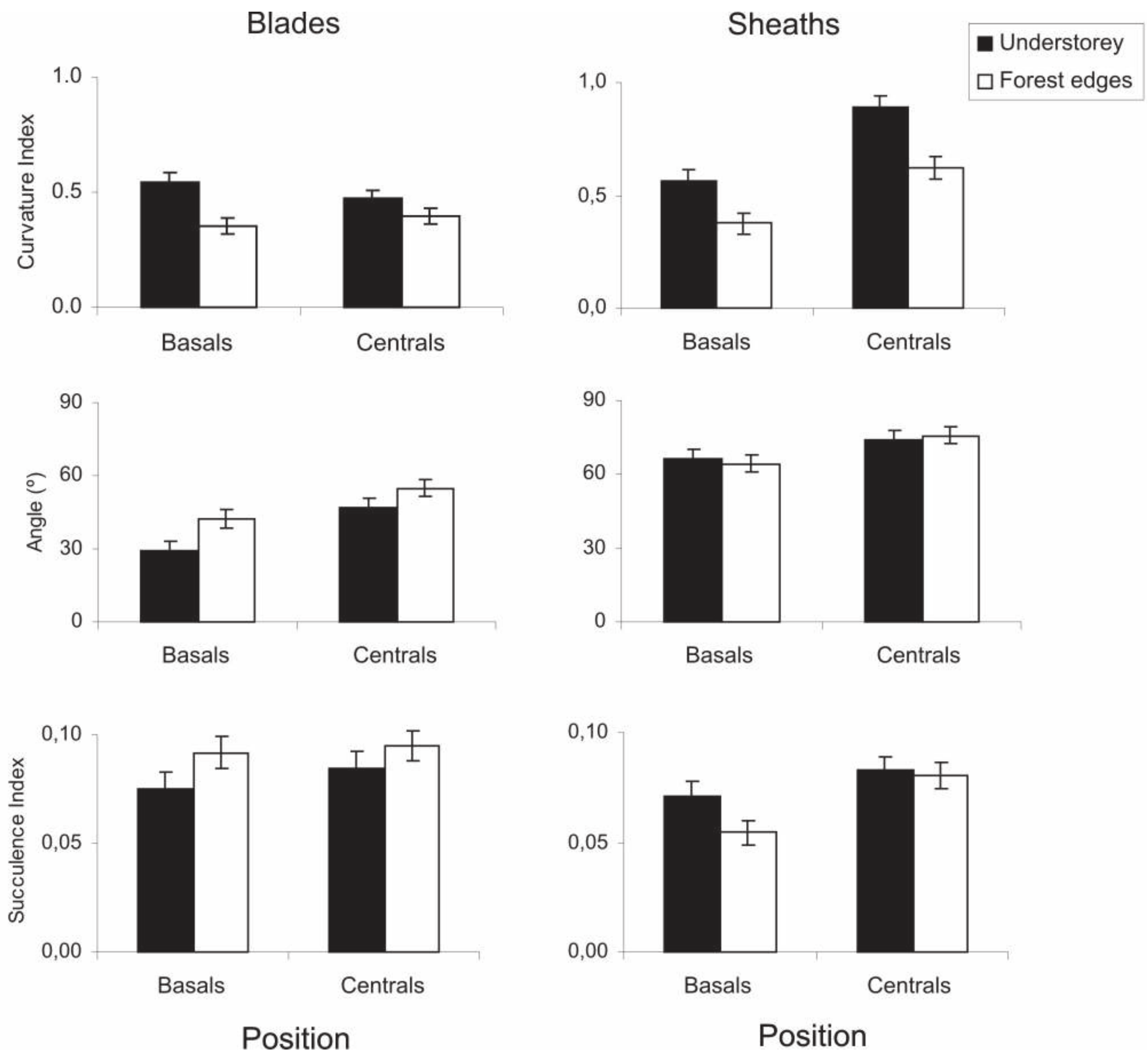

Figure 4. Curvature index, angle, and succulence index (mean ± s.e.m.) of blades and sheaths from basal and central leaves of *Aechmea distichantha* plants from the understory and forest edge.

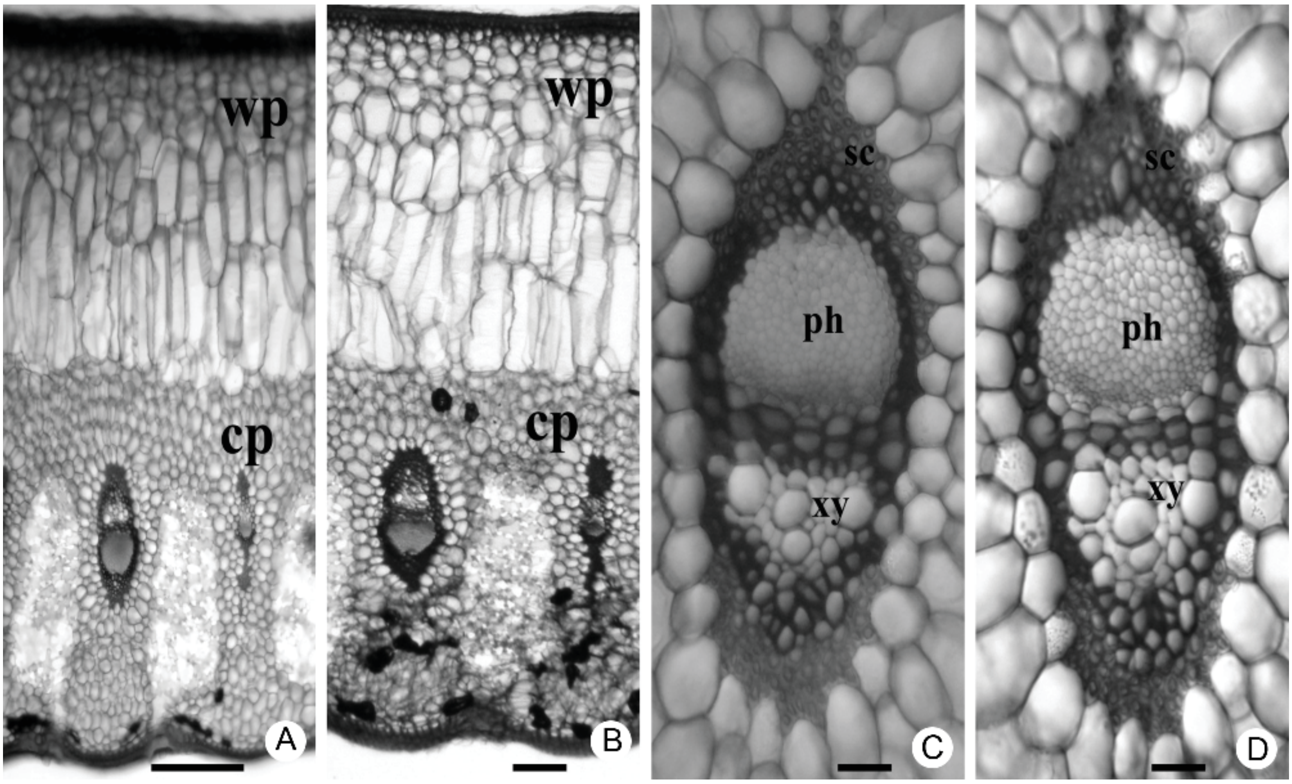

Figure 5. Leaf anatomy of *Aechmea distichantha* plants from the understory and forest edge. A,B Leaf blades (in cross section) showing water parenchyma (wp) and chlorophyll parenchyma (cp). **A.** Cross section of understory leaf. **B.** Cross section of a forest-edge leaf. C,D. Vascular bundles showing xylem (xy), phloem (ph) and sclerenchyma (sc). **C.** Vascular bundle of an understory leaf. **D.** Vascular bundle of a forest-edge leaf. Scale bars = 100µm.

ladares & Pugnaire 1999). The long and narrow blades of understory plants, in contrast, had lower angles in relation to the ground. This linear shape maximizes leaf area while minimizing self-shading (Niklas 1997), but also implies a compromise between carbon gain and the costs of sustaining static and dynamic loads (Read & Stokes 2006). In our study, understory plants of *Aechmea distichantha* reduced bending loads by increasing their flexural stiffness. On the one hand, they could do it by having thicker fiber tissue surrounding the vascular bundles, and on the other by modifying the shape of their leaves (i.e., higher curvature index). Thus, it seems that blades of this understory bromeliad represent a trade-off between photosynthetic leaf area (for light capture) and mechanical support (Read & Stokes 2006).

Forest-edge plants also had more succulent blades than understory plants. A similar pattern has been recorded for other bromeliad species with populations living in sun and shade conditions (Lee *et al*. 1989, Maxwell *et al*. 1992, Benzing 2000, Scarano *et al*. 2002, Skillman *et al*. 2005, Lenzi *et al*. 2006). Succulent and thicker blades are common among bromeliad species living under high light and/or water stress (Benzing 2000). However, it should be taken into account that plants completely exposed to extreme sun conditions may not be acclimated, but stressed (Scarano *et al*. 2002). In our study, thicker blades in forest-edge plants were the result of a thicker chlorophyll parenchyma due to larger cells. It is likely that this is an adaptation for light dissipation, because the shapes of the mesophyll cells and adjacent air spaces are known to influence the paths followed by photons (Benzing 2000). For instance, blades with a palisade transmit larger proportions of incident, high-angle light than blades without a palisade (Vogelmann & Martin 1993). On the other hand, the sheath succulence index and sheath angles of forest-edge plants were not different from those from understory plants. It is likely that these similar patterns arise because the sheaths are not as exposed to light and water stress as the blades, possibly due to their basal locations within the plant and to the ability of the plants to hold water in their tanks (Cavallero *et al*. 2009).

Forest-edge plants had blades with a higher number of stomata than understory plants. Similarly, leaves of *Ananas comosus* plants exposed to 100% light showed a higher stomata density than leaves from plants exposed to 50% light (de Oliveira *et al*. 2008, Batagin *et al*. 2009), and leaves of *Aechmea bromeliifolia* from exposed habitats had a higher stomata density than those from shaded habitats (Scarano *et al*. 2002). This pattern could be related to a higher gas exchange in sun than in shade plants (Pfitsch & Smith 1988, Lee *et al*. 1989, Skillman *et al*. 2005). Forest-edge plants also had higher trichome density on the adaxial side of their blades than understory plants. This could be an adaptation to retard transpiration and to reduce the vulnerability to photoinhibition (Benzing 2000, but see Pierce *et al*. 2001).

Morphology of leaves from different positions within a plant

For both morphotypes the central leaves were the longest and had the greatest length/width ratio. Similarly, oldest and younger leaves of *Ananas comosus* were shorter than those located in between (Krauss 1948-1949) and central leaves of intermediate age of *Vriesea sanguinolenta* showed the maximum length and area (Zotz *et al*. 2002). It is likely that this pattern is associated with plant growth, because basal leaves are the oldest within the plant. When the plant is small and bears a few leaves, they are broad and short and do not overlapped, whereas as the plant grows the leaves become longer and narrower possibly to avoid self-shading (Zotz *et al*. 2002).

Sheath proportion showed the same tendency for both morphotypes. Basal leaves had the highest sheath proportion, despite having shorter sheaths than central leaves. The allocation of more resources to central than to basal leaves seems to maximize plant growth because central leaves have shown a higher photosynthetic rate (Zotz *et al*. 2002).

In both morphotypes, the blade and sheath angles decreased from central to basal leaves, as leaf age increased. A similar pattern was recorded for *Vriesea sanguinolenta* (Zotz *et al*. 2002, 2004). Even though several basal leaves are probably shaded by the longer and narrower central leaves, it is likely that it would not affect plant growth because their photosynthetic rates are lower than those from the central leaves (Zotz *et al*. 2002).

We hypothesized that central leaves would have higher mechanical support than basal leaves. However, there were no differences in curvature index between blades from both positions, despite large differences recorded in their blade lengths. An alternative explanation is that central leaves may increase their flexural stiffness by having thicker fiber tissue surrounding the vascular bundles than basal leaves. However, because we did not do anatomical studies for the basal leaves, this needs to be further researched.

CONCLUSIONS

We found large morphological, architectural and anatomical differences between leaves from understory and forest-edge plants. Understory plants increased their flexural stiffness by having thicker fiber tissue surrounding the vascular bundles, and by modifying the shape of their leaves (i.e., higher curvature index). Therefore, it seems to be a trade-off between photosynthetic leaf area (for light capture and water use) and mechanical support. Finally, our results showed that phenotypic plasticity recorded at the plant level for *Aechmea distichantha* (Cavallero *et al*. 2009) originates as a "bottom – up" mechanism at lower hierarchical levels, such as the anatomical level and leaf level.

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